ORIGIN, EVOLUTION, AND DISTRIBUTION OF THE NEOTROPICAL ACRIDOMORPH FAUNA (ORTHOPTERA): A PRELIMINARY HYPOTHESIS

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INTRODUCTION

The existing knowledge of the Neotropical fauna of acridomorph insects (Proscopiidae and Eumastacidae included), especially in regard to its systematics, geographical distribution, and paleontology, does not allow us to ascertain the past history or origin of its elements. A recent renewal of interest in its study, however, has resulted during the last few years in a number of important papers (mainly by Amedegnato, Descamps, Kevan, Roberts, and Ronderos) that substantially contribute to our knowledge and provide a basis for interpretacion.

The recent works are based on the considerable volume of research accumulated by the scientists who laid the foundations of Neotropical acridiology, such as Bolivar, Bruner, Brunner von Wattenwyl, Burmeister, Giglio, Tos, Hebard, Liebermann, Rehn, and Stal, to mention only the most prominent. The aforementioned recent studies allow us to systematize and understand better the data provided by the older papers.

Among the recent contributions to the systematics of the Neotropical Acridomorpha are those of Amedegnato (1974 principally) that have become indispensable for any attempt at interpretation of the fauna's origin and distribution. Without Amedegnato's classification, the present paper and similar contributions would be impossible. Unfortunately, Amedegnato's complete thesis, of which the mentioned 1974 paper is only a small part, has not yet been published. Judging only by her classification, it seems to me that said thesis will be the most important contribution of recent times to the systematics of the Neotropical acridomorphs.

Also during the last ten or fifteen years, in an entirely different field of knowledge, important advances have been made that have a decisive bearing on interpretation of evolution and zoogeography. I refer to recent research in geophysics, particularly as related to continental drift and plate tectonics. Together with modern studies in paleogeography, paleontology, and stratigraphy, they allow us to interpret the known facts about the Neotropical biota in a different and more rational way. These interpretations will probably be closer to the truth than the previous ones that were based on the idea of fixed, invariable relative positions of the continents, islands, and oceans throughout geological time.

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Modern knowledge of the stratigraphy and paleontology of Central America and the northwestern corner of South America particularly provides a more adequate picture of the relationships between North and South America and hence, of the possibilities of biotic interchange from the Cretaceous to Recent times. This contributes to a more adequate knowledge of the origin of the South American fauna.

Another relatively new piece of information that cannot be ignored anymore for interpretation of the evolution of the South American fauna is the probability that the Pleistocene glaciations influenced in a radical way the climate and distribution of the plant formations and corresponding fauna during the aforementioned epoch. A series of alternating periods of cold and dry and warm and humid climates caused corresponding retreats and expansions of tropical rain forest. During glacial periods, this jungle was reduced to a series of "islands" or "refuges", located mainly at the periphery of the present Amazon basin. Other plant formations such as the prairies or the Andean paramos underwent a similar process but in the opposite phase, expanding and coalescing during the glacial periods, retracting and fragmenting during the interglacial ones. These episodes determined the isolation in "refuges" of the elements of the tropical biota, and lead to the corresponding speciation and later re-mixing of the resulting species in interglacial periods such as the present one. The myth of the immutability of the tropical jungle has been destroyed, and, in this way, the richness and multiplicity of its species can now be understood. The concept of a series of episodes of isolation and re-union in the course of time with respect to important sections of the Neotropical fauna must be incorporated now into any attempt at interpretation of the origin and composition of the present fauna of the region. It is possible that, for the invertebrates, this concept may be even more important than for the vertebrates. For information on this subject, see Haffer (1967), Vanzolini & Williams (1970), and Vuilleumier (1971).

The part of the Neotropical fauna whose origin and evolution is probably best known is the vertebrate fauna and, within it, the mammals. On account of their evolution in relatively recent times, of their generally large size, and of the facility with which their skeletal remains become fossilized, the paleontology of mammals is relatively well known, and make possible the most complete and coherent interpretations available of the origin and evolution of the Neotropical fauna.

Therefore, the facts related to the evolution of the Neotropical mammals and the interpretations of their present distribution cannot but influence the thinking of those who endeavour to understand the past history and the present distribution of other zoological groups. It is necessary to be wary, however, of the tendency of translating verbatim to other groups of animals -and particularly to invertebrates- knowledge obtained from the study of mammals. Mammals and insects have undoubtely different possibilities of migration and distribution, of survival or extinction under changing climatic conditions, etc. Also, insects are a much older group, and this should be kept in mind when we study the origin of regional faunas. Evolution in situ from very old stocks may be probable in regions where the presence of other animal groups may be attributable to migration.

Consensus of opinion indicates that, as in the case of the mammals, a primitive acridomorph stock already have existed during the Jurassic as an offshot of, or alongside, the predominantly Mesozoic Locustopsidae. Contemporarily with the primitive pantothere, triconodont, and other primitive mammals, there were eumastacids recorded from the Upper Jurassic of Asia (Sharov, 1968). But even if we put these primitive lines aside, it seems that the acridids, which are the dominant group of the recent acridomorph fauna must have evolved in the Cenozoic. Acrid evolution in the Neotropical region may have been influenced by the same geophysical, geomorphological, climatic, and other events that influenced the evolution and distribution of mammals.

It is relevant to this subject also to mention the rather widespread, incorrect notion that the main source -if not the only one- of the South American biota must be sought in the northern continents. A stream of life from the rich northern lands to the barren southern ones is supposed, by some authors, to be the origin at most of the southern biotas. I have been unable to find, however, a suitable explanation of why Laurasia might have been so rich in life, while the enormous Gondwanian continent should have been as poor as it has been postulated. The one factor that comes to mind is that scientific

thought has been unduly influenced by the far better knowledge of the fossil faunas of Eurasia and North America, as compared with those for the southern continents. Also, maybe the notion is valid for some well-known faunal groups and has been unduly extrapolated to include others. A reaction against the idea, mainly in the form of research in the paleontology of the southern lands, has fortunately set in, and it is likely the end result will be to prove that the idea a misconception, at least for many zoological groups.

The present paper is intended only as a preliminary hypothesis on the origin, evolution, and geographical distribution of the Neotropical acridomorph fauna. I believe the premises on which this hypothesis is based to be true and sound - h as the classification of the Neotropical acridomorphs by Amedegnato, and also the ormation on other subjects about which I lack the power of critical examination, suc as those related to geophysics, paleogeography, paleontology, stratigraphy, etc. Unfortunately, the soundness of these premises does not guarantee the truth of my own ideas. Whatever is true in them, however, must come from the said premises, while I myself am responsible for the errors. I am aware that my interpretation of these things is highly speculative and that, in the best of cases, it will be modified in the future or discarded altogether. If it promotes further speculation and the study of this very interesting subject, it would have the right to claim some usefulness, even in case it proves to be entirely mistaken.

SOME FACTS ABOUT THE HISTORY OF THE NEOTROPICAL REGION.

The replacement in scientific thought of the concept of a permanent, unchanging relative position of the continents for an idea that admits the mobility of the land masses has a decisive bearing on the interpretation of the origin and history of the biota of the Neotropical region.

Until the middle sixties, and in spite of a growing tendency of the geophysical sciences toward the theory of continental drift, interpretations of the history of the Neotropical fauna were based on the premises of continental stability. Continents and oceans, it was assumed, had been practically where they stand now, at least during the time that incompasses the history of that fauna. Among the authors who have given the most cogent interpretations of the history of the Neotropical fauna, Simpson (1950-1965) and Darlington (1965) seem inclined to think that continental mobility is unnecessary for any explanation of the history of this fauna, and they discredit the idea of continental drift. At least in the case of Simpson, this comes from the circunstance that he deals mainly with the evolution of mammals during the Cenozoic, and during this era the intercontinental relations of the Americas were not too different from those of the present time. Also, it is fair to say that these excellent papers were written at a time when present concepts of continental drift and plate tectonics were in a state of preliminary research and discussion and were far from being generally accepted as they are today.

According to the recent geophysical data on continental drift, plate tectonics, paleomagnetism, sea floor spreading, etc., accumulated mainly during the last fifteen years, the movements of the continental masses from the end of the Paleozoic to the present have been ascertained with relative accuracy and cannot be ignored in any study of paleobiotas. Likewise, the knowledge of the geological history and paleontology of Central America and the northwestern corner of South America has been increasing steadily during the last two decades and now provides a fairly complete idea about the different stages of these regions throughout the Cenozoic and, hence, of the contacts and relationships between the Americas during the era.

The sources of this knowledge are, of course, many, and lacking expertise in these fields I have used for this paper mostly scientific compilations of information rather than the original papers themselves. In the text that follows, I do not make specific references to the source of each bit of information quoted, as I do later on with reference to the particular subject of the acridomorph fauna. The papers that have been used referring to geophysics, paleontology, evolution, geography, and geology are mainly those of Colbert (1955), Dewey (1972), Dietz & Holden (1970), Hallam (1972), Harrington (1962),

Hibbard (1960), Kurtén (1969), Laurentiaux (1953), Nygren (1950), Patterson & Pascual (1968), Raven & Axelrod (1975), Sauer (1950), Whitmore & Stewart (1965), Wilson (1963), and Woodring (1966). According to the information provided by these authors, I consider the following facts most significant in relation to the past history of the Neotropical acridomorphs.

At the beginning of the Mesozoic, in the Middle to Upper Triassic (200 million years ago), all the emergent lands that form the continents of the present time were united in a single supercontinent that has been called Pangaea (see figures 1 to 6 with reference to the text that follows). In that supercontinent, what is now South America was in direct contact with North America in the north, with Africa in the east, and with Antarctica in the south, and, indirectly, with the rest of the continental lands.

By this time, the evolution of the insects as a class was already fairly advanced. The world insect fauna was then composed of a mixture of primitive and relatively modern forms, some having originated in Laurasia, some in Gondwana. Except for the parts then covered by shallow continental seas, the possibilities of migration and territorial interchanging of these faunas must have been limited only by climatic and ecological conditions. There is no reason to suppose that the southern or Gondwanian insect fauna was then poorer than the northern or Laurasian one. The fossil record for the insects is such an incomplete and fragmentary one that the lack of fossil evidence cannot be taken as proof of the absence of a group of insects in a certain part of the world. The past history of insect faunas must necessarily be deducted in many cases from careful study of the recent ones.

Data on the sequence of events that took place after the beginning of the Mesozoic and resulted in the breakup of Pangaea and the subsequent drifting of the resulting continental land masses to their present positions are not completely in accord, and, as yet, it seems evident that some details remain obscure. In the summary of these events below, I have followed mainly Raven & Axelrod (1975) for the series of geophysical occurrences that influenced the faunal history of the Neotropical region.

The most important land connection of South America in regards to the oldest part of its biota must have been the connection with Africa, with which it was completely united before the appearance of the Atlantic Ocean. Because that connection was broken a long time ago (90 million years), however, relationships between the faunas of both continents must have been, by now, masked by a long period of separate and independent evolution and, in consequence, are difficult to trace at present. The past faunal continuity must be more significant in the case of the invertebrates, many of which were, by the end of the Paleozoic, much more highly evolved than most terrestrial vertebrates.

The Atlantic rift first appeared between the southern parts of South America and Africa some 140 million years ago, near the limit of the Upper Jurassic and the Lower Cretaceous. This rift widened in the south as it advanced northwards, and finally Africa

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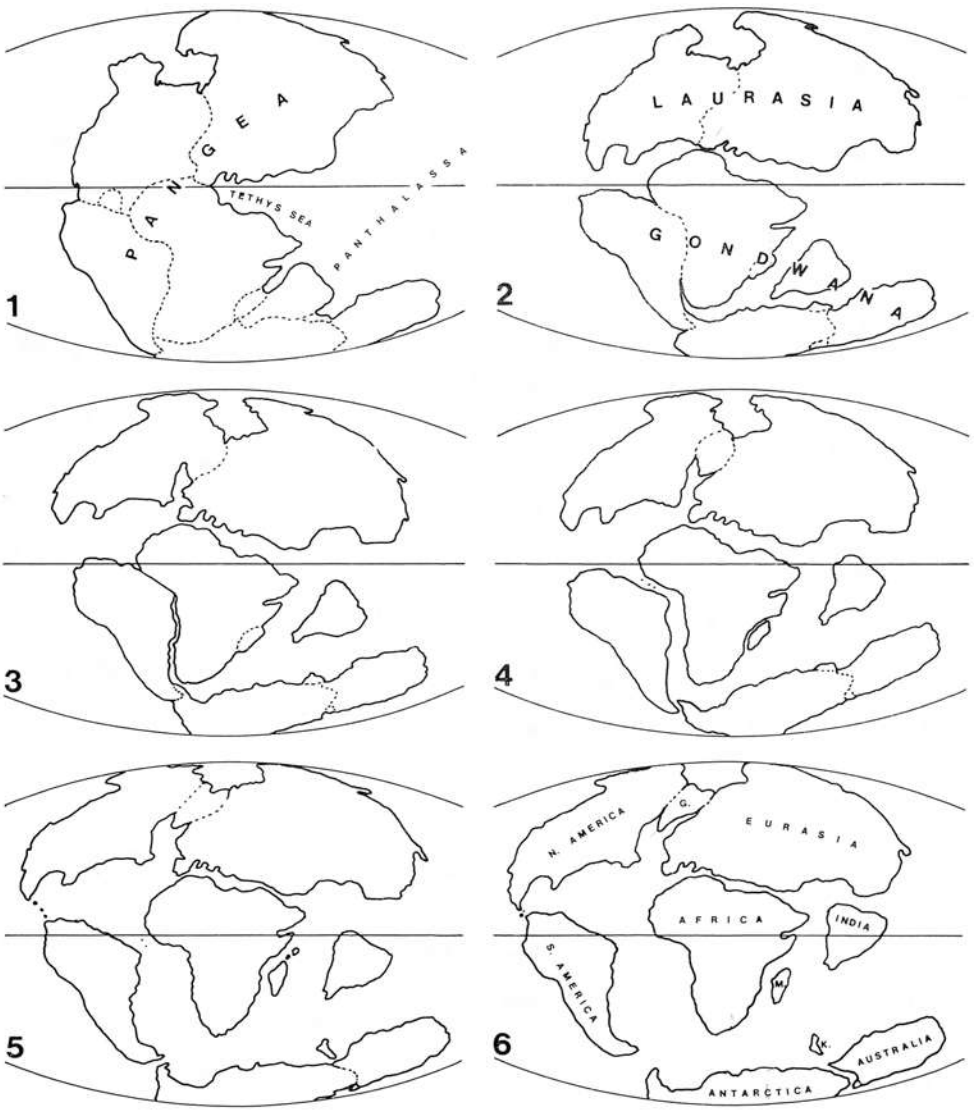
Fig. 1. Reconstruction of the supercontinent of Pangea as it may have been at the beginning of the Mesozoic, 200 million years ago. What is now South America was then directly united to North America, Africa and Antarctica, and through them to the rest of the emergent lands. Many faunal elements must then have been common to the three named continents, and other might have been widespread over all or most of Pangea, as it seems to be the case with the Locustopsidae, which are considered to be ancestral to all Acridomorpha. Fig. 2. Sometime between the end of the Jurassic and Lower Cretaceous, 150-140 million years ago, Laurasia in the north and Gondwana in the south became separated. Gondwana itself had already started to break up, with the drifting northwards of India, a rift between southern Africa and Antarctica, and the Atlantic Rift starting between the southern parts of Africa and South America. South America and Africa must have had many faunal elements in common at this time, when insects were already fairly evolved. Fig. 3. After the end of the Jurassic, 130 million years ago, the Atlantic rift had reached what is now the Gulf of Guinea, but South America and Africa were still united in the north. North America was then separated from the nearest point of South America by some 3000 kmts of open ocean. A periantarctic biota, whose relicts are still notable et present, must have flourished at this time. Fig. 4. Near the end of the Middle Cretaceous, 90 million years ago, South America began a long period of isolation from all other continental lands. The Atlantic Rift had already separated it from Africa, and direct land connections



with Antarctica were also broken. Many faunal groups that South America must have shared with Africa and with Antarctica + Australia began then a long period of separate and independent evolution in their respective territories, that must have by now made their primitive relationships difficult or impossible to trace. Fig. 5. At the close of the Cretaceous, 65 million years ago, South America was still an island. Africa was already some 600 kmts away at its nearest point. Between North and South America, the ocean had narrowed to 1300 kmts, and a chain of volcanic islands had appeared between then. From this time on, both continents drifted closer and islands must have become more abundant, making possible at some time a limited interchange of certain faunal elements which could traverse relatively short distances over the sea, either by flying, swimming or as waif immigrants. Fig. 6. In early to Middle Tertiary times, Africa and South America had drifted farther apart, but the latter had considerably approached North America, not only by drift but also by the emergence of lands in what is now Central America. Much later, near the close of the Pliocene (5,6 million years ago) a land connection between both continents was finally established, that was the corridor through which important faunal exchanges too, place.
(Figures 1 to 6, after Dietz and Holden, 1970, modified).

and South America became separated in the north (Guiana Shield) about 90 million years ago, near the end of the Middle Cretaceous. At the close of the Cretaceous, 65 million years ago, the shortest distance between S America and Africa (in the north) was around 600 kmts., and volcanic islands on and around the Mid Atlantic Ridge probably still formed a link between them.

Indirect connections of South America with Madagascar and India, through the African continent existed in the Paleozoic, and, of course, must have ceased with the separation of Africa and S. America. This connection may have been broken erlier if the separation of India and Madagascar from Africa took place before that of Africa with South America. Different authors do not agree in dating these events. Dietz & Holden state that India had already drifted wide of Africa + Madagascar by the end of the Triassic, while Raven & Axelrod say that they were still united in Middle Cretaceous. Madagascar was probably still united to Africa after the drifting away of India until about the end of the Cretaceous. The union of South America with Antarctica and Australia was a significant one from the viewpoint of the biota.

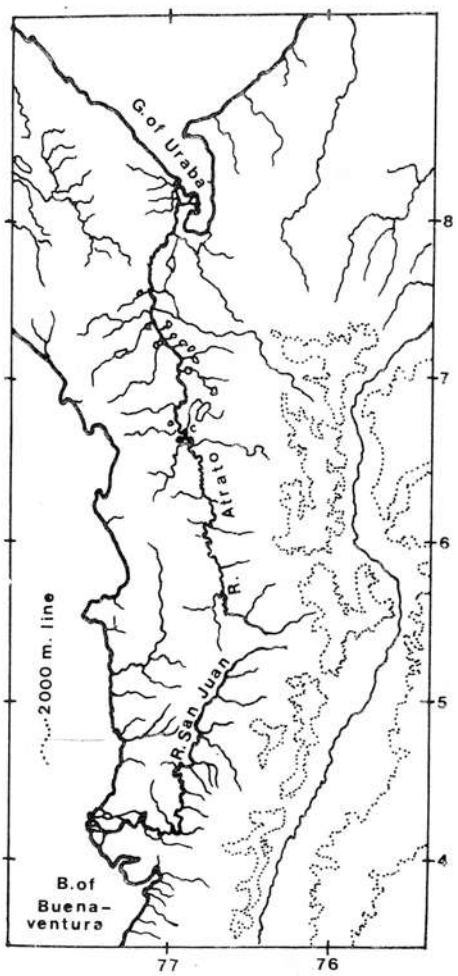


Fig. 7. The land bridge of Panama, that since Pliocene times communicates Central and South America. In the axis of the now emerged Bolivar Geosyncline, covered by the sea until Mid-Pliocene, flow the Atrato and San Juan Rivers, in the rainiest part of South America. The only overland route between them is the narrow passageway by the headwaters of both rivers, roughly midway between parallels 5 and 6. (After Hershkovitz, 1966).

A close relationship between elements of southern South America and the Australian-Tasmanian and even the New Guinean and New Zealandian faunas is evident and has been the subject of much research. At the time of union with South America, Antarctica was located north of its present position. Its northern edge, at least, then had a temperate climate, as the study of its fossils has shown. Its role as a passageway to and from Australia and other eastern lands must therefore, have been important even if only faunae of temperate climates could pass through it. The break between northern Antarctica and the southern end of South America probably took place before the end of the Cretaceous, some 85 million years ago, but these lands remained in close proximity for a long time afterwards, and indirect connection through islands (finally broken by distance and cold) persisted until about the end of the Eocene, 38 million years ago. Regarding the overland connections of South America with other continents, the one with Africa was broken about 90 million years ago; that with Antarctica maybe a little later, 85 million years ago. Thus, South America was an island continent for about 80 million years, until a new land connection with N. America, the Panamanian Land Bridge, was established approximately 5,6 million years ago.

In regard to the relationships between North America and South America, the following events are of importance. A wide union of the continents in what is now the Caribbean region existed since some undetermined time in the Paleozoic, and lasted until the breakup of Pangaea. Details of that union in what is now the Gulf of Mexico and the Caribbean Sea are, however, obscure. The connection probably broke at the close of the Triassic, some 190 million years ago, and, from that moment, the continents drifted rather rapidly apart. Separation of North and South America was probably roughly coincident with the drifting apart of the whole of Laurasia from Gondwana, which remained separated until relatively recent times. Separation of North and South America reached a maximum of 3000 kms. during Middle to Upper Cretaceous. This distance was wider than the shortest present distance between Africa and South America.

Toward the end of the Cretaceous (approximately 65 million years ago), South America and North America were still separated by some 1300 kms. of ocean, though there probably existed a chain of volcanic islands between them that became more numerous in the course of the Tertiary. Probably after the close of the Cretaceous, what are now the northern and middle parts of Central America began to emerge from the waters that covered them before. The distance between North and South America gradually diminished, and the number of intervening islands increased until actual contact between both continents took place in Middle to Upper Pliocene, some 5,7 million years ago. Also in the Pliocene, the rising of the Andean Chain began. First proximity and later actual contact between the Americas at the Isthmus of Panama, and also the rising of the Andes, are elements of importance for the history of the Neotropical biota.

With regard to the actual union of the two continents, the geophysical, paleogeographical, stratigraphic, and paleontological data seem at present to indicate:

a) North and South America were widely separated during most or all of the Cretaceous (70 million years). Hence, the possibilities of migration of animals from one to the other of these continents during Cretaceous times were, in the best of cases, slight. The Atlantic and Gulf coastal plains of North America, including Florida, were under water until the Oligocene, making the gap between the continents even greater.

b) By the beginning of the Tertiary (65 million years ago), 1300 kms. of open ocean still separated the southern end of North America (what is now northern Nicaragua) from the northwestern coast of Colombia. Emergence of lands that took place at the close of the Cretaceous had formed the northern part of Central America, but the rest of it was still under water. Additional land emerged during the Tertiary forming part of Panama, which was just a peninsula of the North American continent until Mid-Pliocene.

c) Stratigraphic and paleontologic studies reveal that the north western corner of Colombia was constantly covered by water from the Upper Jurassic to the Paleocene. Between the Eocene and Lower Oligocene, the opening of the Bolivar Geosyncline was the last obstacle for the union of Panama and Colombia. The botom of this geosyncline did not completely emerge until Mid-Pliocene, when a direct land connection between

North and South America was finally established. Earlier connections have been postulated, but stratigraphic and paleontological data make them improbable. The differences of the Miocene mammal faunas of southern Panama (fossil beds of Cucaracha) and northern South America (La Venta and other localities) are very clear, the Panamanian fauna being composed exclusively of nearctic mammals, while those of the Colombian and other northern South American localities consist only of South American ones. Likewise, the Miocene marine mollusks in the Caribbean and Pacific sides of Panama are identical, showing that these waters had not yet became separated by a barrier of land.

Another important fact regarding the neotropical fauna was actual contact between North America and Asia in the region of today's Bering sea that existed for most of the Cenozoic. The climate of this region during at least part of the Cenozoic was much milder than nowadays (Hibbard, 1960). Several well documented migration of mammals took place over this land bridge, and the same occurred with other faunal elements.

The possibilities of faunal migration between continents are not limited to and do not necessarily coincide with periods of actual contact between them, as it has been repeatedly pointed out by zoogeographers. Many animals are able to cross extensions of water, either by swimming, flying, or in a passive way on floating plant rafts, driftwood, or other floating debris. The mere proximity of lands and the presence of intervening islands greatly increase the chances of migration. An actual land bridge may prove impassable to many animals because of adverse climatic or ecological conditions. Deserts, high mountain chains, or intense cold are effective barriers in most cases, on spite of land continuity. Even in cases far rwoved from these extremes, the conditions of climate and vegetation prevalent in the regions of communication between continents -such as the Cenozoic Bering bridge or the Pleistocene to Recent one of Central America- may have the effect of a filter, making difficult or impossible the passage of organisms that are unable to adapt to or withstand, even temporarily, the climatic and ecological conditions in the corridor.

With regard to the possibilities of migration to or from South America and the neighboring lands, the circumstances referred to above seem to indicate the following:

a) Opportunities for migration between South America and Antarctica -or Australia via Antarctica-were direct overland until Upper Cretaceous, 85 million years ago. Indirectly through island chains, limited possibilities of migration probably existed until the beginning of the Oligocene, 38 million years ago.

b) Direct land connections between North and South America existed from an undetermined age in the Paleozoic until the close of the Triassic, approximately 190 million years ago. These continents drifted apart more or less rapidly in the Jurassic, and during the whole of the Cretaceous some 3000 kms. of sea extended between them. As has been noted, the possibilities of animal migration between them increased during the Tertiary as the two continents came closer by drift, by the emergence of lands in southern North America, and by the formation of chains of volcanic islands between them until direct contact was established in the Pliocene, , 5,6 million years ago.

c) Direct overland migration of faunae to and from the northeastern part of Asia and North America by the Bering bridge existed probably for a good part of the Cenozoic. Faunal interchange between Asia and South America by this route certainly took place in late Cenozoic.

d) Even if it may be inferred that the most important connection of the South American continent with regard to faunal migrations in relatively modern times was the Central American bridge, in the older strata and the so-called autochthonous elements it is necessary to consider also the Gondwanic fauna of the Paleozoic and Mesozoic eras, and the continuity of lands of this enormous continent that made possible the migration of faunas between its different regions.

e) Doubtless, the establishment of a direct overland connection between North and South America in the Pliocene allowed for important faunistic interchange between the continents, as has been clearly shown, especially by the study of the mammal faunas. However, the humid tropical conditions prevalent in Central America are an important barrier for animals of temperate regions. Even now, direct terrestrial route between

Central America and northwestern Colombia presents insurmountable difficulties for many animals. The Pacific coast of Colombia, with 6000 to 8000 millimeters of yearly rainfall, is probably the rainiest region of South America. Parallel to this coast runs the axis of the ancient Bolivar Geosyncline, occupied by the basins of two important rivers always full to overflow by torrential rains: the Atrato River flowing to the north, going to the Bay of Urabá, in the Caribbean Sea, and the San Juan River going south to the Pacific coast north of the Bay of Buenaventura (Fig. 7). The only passageway between the two basins is a narrow strip of land by the headwaters of both rivers. It is difficult to imagine animals of dry or temperate climate successfully migrating through this kind of land. However, some have done it, such as the acridomorphs of some groups that will be mentioned below (particularly the Melanoplinae and the Oedipodinae). A plausible explanation is that, during the Pleistocene glaciations, the climate of this region may have been far more favorable for the migration of such animals than it is at present.

ORIGIN AND EVOLUTION OF THE ACRIDOMORPHA

After the above sketch of the principal external elements that are important for understanding the origin and evolution of the Neotropical acridomorphs, especially the South American ones, it is convenient to examine the scanty available knowledge on the origin and evolution of these insects in general. The fossil specimens that have been found to date are few, and what is known about their evolution is more the result of deductions and comparisons of recent forms among themselves and with the few fossil ones than the outcome of a direct study of their fossil record.

The origin of the Acridomorpha seems certainly related to the Mesozoic family Locustopsidae. Sharov (1968) considers the Locustopsidae as the direct ascendants of the Caelifera (Fig. 8). The Locustopsidae appear in the fossil record in the Lower Triassic and are found throughout the Triassic, Jurassic, and Lower Cretaceous, to disappear at the close of the Middle Cretaceous. According to Sharov (loc. cit.), fossil Locustopsidae are found in the Triassic and Jurassic of Siberia, in the Jurassic of western Europe, and also in the Upper Jurassic of Australia. If we consider the shape of Pangaea during the Jurassic (Fig. 1), Siberia and Australia were then the regions fartherest apart of the supercontinen by an overland route. A wide portion of the Panthalassa and all of the Tethys Sea interposed between them. This suggests that the known fossil record of the locustopsids must be fragmentary, and that they must have had a much larger distribution, probably being widespread over most of Pangaea, or at least over the territory along its oriental coast. The mentioned author indicates that some locustopsids already show acridoid characters in the structure of the tarsi, antennae, and ovipositor. Some Cretaceous species also approach the acridoids in the structure of the hind wings. This leads him to consider the locustopsids as the origin of all the acridomorphs and of the Caelifera in general.

Also according to Sharov, the Eumastacidae arose from the Locustopsidae in the Lower Jurassic; the basic stock of all the Acridoidea evolved at the limit of the Lower and Middle Jurassic; and the Pneumoridae and possibly the Proscopiidae (families that this author considers to be related) originated in the Middle Cretaceous near the extinction of the locustopsid stock (Fig. 8). The basic stock of all the Acridoidea *sensu stricto* (exclusive of Eumastacidae, Proscopiidae, and Pneumoridae) would be, according to this author, of Jurassic origin, but the diversification and expansion of these insects did not take place until the Tertiary, simultaneously with the appearance of prairies and further increased by Mid-Oligocene with the spread and develpment of steppe and semidesert. Fossils of acridoids are known from the Oligocene, represented by species not too different from Recent ones.

Ragge (1955) deducts, on the basis of the study of wing venation, that the locustopsids and the acridomorphs must be related by common origin rather than by direct descent. According to his opinion the Locustopsidae, Pneumoridae, Eumastacidae,

and Acrididae arose at the end of the Paleozoic from an unknown, primitive ancestral stock. The probably Pangeic distribution of the Locustopsidae does not help to clarify this problem whether we consider the locustopsids as direct predecessors of the acridomorphs or as a parallel line of common ancestry.

The presence in South America of certain relatively primitive acridomorph groups such as the Proscopiidae and the Tristiridae that do not exist in other regions of the world seem to be indicates that at least a part of the primitive stock of acridomorphs was already in Gondwana when it separated from Laurasia at the end of the Triassic. It may also be possible that the Acridomorpha are to some extent polyphyletic, and that several of the Recent groups come from slightly different branches of an older pre-acridomorph stock, related in some way to the Mesozoic locustopsids. Recent classifications of the Caelifera such as that of Uvarov (1966), which separates the Eumastacidae, Proscopiidae, Tanaoceridae, and Pneumoridae from the superfamily Acridoidea, or that of Dirsh (1975), that erects the Eumastacoidea (Eumastacidae + Trigonopterygidae + Proscopiidae) as an order separate from the Acridomorphoidea within the superorder Orthopteroidea, suggest a certain plurality of origins at least for these cases. Within the South American fauna, the Proscopiidae, Tristiridae, and the combined Ommexechidae + Romaleidae could be the descendants of three different branches of primitive Gondwanian acridomorph or pre-acridomorph stock.

RECENT ACRIDOMORPHS OF THE NEOTROPICAL REGION

The composition of the Recent fauna of Acridomorphs in the Neotropical region indicating families and, in the case of the family Acrididae, also subfamilies, is shown in Table Nº 1. This table is not arranged according to phylogeny or affinities, but rather in relation to ideas on the origin of the differente groups that will be referred to in the text that follows. For each of the families and subfamilies, the approximate number of Neotropical genera has been indicated except in the case of the Romaleidae, in which the total number of the American genera is included. The cassification used in this table is, in general, according to Amedegnato (1974), with some slight modifications, notably the inclusion of the genera of the Aucacrini with the Ommexechidae, rather than with the Romaleidae. The names of families that are not found outside the Neotropical region (except for a few genera that have invaded the south of the Nearctic region) have been marked with an asterisk (+). In the case of the family Acrididae, the same applies to the names of the subfamilies.

Examination of this table shows that, of the eight families found within the Neotropical region, three (Eumastacidae, Pyrgomorphidae, and Acrididae) are shared with the rest of the world. The other five (Proscopiidae, Tristiridae, Ommexechidae, Romaleidae, and Pauliniidae) are exclusively Neotropical and probably of South American origin, and as such, have been marked with an asterisk. The family Acrididae as a whole is, of course, represented elsewhere in the world, but within it there are two different groups of subfamilies. The first of these groups comprises five subfamilies that have been marked with an asterisk (Proctolabinae, Copiocerinae, Leptysminae, Rhytidochrotinae, and Ommatolampinae) because they are not represented outside of the Neotropical region (except for a few genera in the south of the Nearctic region). If they are outsiders to the Neotropical region, as their acridid relationships could indicate, they must come from very old immigrants, and a considerable part of their evolution must have taken place in the Americas. The remaining five subfamilies (Melanoplinae, Cyrtacanthacridinae, Acridinae, Gomphocerinae, and Oedipodinae) are represented elsewpere in the world, and must be rather recent additions to the Neotropical fauna. Each family and, in the case of the Acrididae, each of the different subfamilies pose peculiar problems, as will be shown below.

Table Nº 1. Composition of the Neotropical acridomorph fauna, indicating for each family or subfamily the number of known Neotropical genera. Nearctic genera have also been included in the case of the Romaleidae. Classification slightly modified after Amedegnato (1974).

Families and subfamilies	Number of genera included in each
PROSCOPIIDAE+	17
TRISTIRIDAE+	17
OMMEXECHIDAE+	13
ROMALEIDAE+	63
PAULINIIDAE+	2
EUMASTACIDAE	20
PYRGOMORPHIDAE	5
ACRIDIDAE	191
PROCTOLABINAE+	22
COPIOCERINAE+	11
LEPTYSMINAE+	22
RHYTIDOCHRTINAE+	15
OMMATOLAMPINAE+	46
MELANOPLINAE	22
CYRTACANTHACRIDINAE	2
ACRIDINAE	14
GOMPHOCERINAE	30
OEDIPODINAE	7

AUTOCHTHONOUS NEOTROPICAL FAMILIES OF SOUTH AMERICAN ORIGIN
(Proscopiidae, Tristiridae, Ommexechidae, Romaleidae, Pauliniidae)

According to their distribution whithin the Neotropical region, this assemblage of families seems, to be strictly of South American origin. Most of them originated near the southern end of South America. Among them the family Romaleidae, with 63 known American genera, is the largest and most diversified. The Proscopiidae is distributed throughout South America and is practically limited to this continent. The Tristiridae, with 17 genera, is clearly of southern South American origin. The Ommexechidae, with 13 genera, is also of South American distribution, and the Pauliniidae is a very small, probably artificial family of doubtful affinities.

Proscopiidae. This typical South American family is aberrant with regard to the rest of the Acridomorpha, which has lead most authors to separate it from the true Acridoidea. Mello Leitao (1939) points out certain similarities of the proscopiids with the Neotropical pyrgomorphid genera *Omura* and *Algete* but does not suggest further affinities between them, which would be, of course, unwarranted.

A close relationship between proscopiids and eumastacids has been repeatedly suggested. Westwood in his "Arcana Entomologica" (1843, vol. I, p. 99; vol. II, p. 54), was probably the first to indicate a relationship between *"Mastax"* and *"Proscopia"*. This opinion of Westwood has not been quoted afterwards, to my knowledge, but the same relationship has been indicated by several later authors. C. Bolivar (1930) says that "the eumastacids, together with the proscopiids and the pneumorids, form a natural group within the Acridoidea, because of the lack of abdominal auditory organs, and the shortened antennae". Rehn (1952) suggest a relationship betwean the proscopiids and the eumastacid subfamily Morabinae. Dirsh (1961) indicates that the proscopiids do not have a close relationship with the other families of acridoids, and suggests that they represent an early branch of an unknown pre-acridoid stock, with remote affinities with the eumastacids. Randell (1963) points out similarities between the female reproductive structures of proscopiids and eumastacids.

Recently, Blackith & Blackith (196) presented a table comparing the external characters of the Morabinae with those of the proscopiids, pyrgomorphids, and acridids, pointing to a marked similarity of the first two groups. Kevan (196) formally erected the superfamily Eumastacoidea with the families Eumastacidae and Procopiidae. Dirsh (1973) erects the order Eumastacoidea with the eumastacids and proscopiids and also the locustopsids and trygonopterigids. Sharov (1968) places the proscopiids and pneumorids together in his superfamily Pneumoroidea.

It seems evident from the above that a majority of the opinions relates the proscopiids and eumastacids, mainly through the eumastacid subfamily Morabinae. Descamps (1974), however, from a study of the genitalia of nine genera of proscopiids and their comparison with that of the majority of the genera of Eumastacidae, concludes that the two groups are unrelated, and that different and independent superfamilies should be erected for them. This latter author remarks that the proscopiids, an autochthonous South American group, could not be related to the South American eumastacids, which are recent invaders of Oriental affinities. He also denies for them, on the basis of their genitalic structures, any relationship with the Australian Morabinae.

The phyletic origin and relationships of the Proscopiidae cannot yet be clearly defined with the available information. It is evident that the proscopiids are an ancient group with little affinity with the rest of the acridomorphs. Their geographic origin lies in the southern part of South America, and from there they have spread to the rest of this continent, with one species reaching Central America (Panama and Costa Rica) and another the island of Bonaire. Liana (1972), who accepts their relationship with the Morabinae, proposes for both groups a common paleoantarctic origin. If a relationship with the Morabinae does not exist, as Descamps states, the proscopiids probably descended from a primitive acridomorph stock isolated since the beginning of the Mesozoic in the southern part of South America.

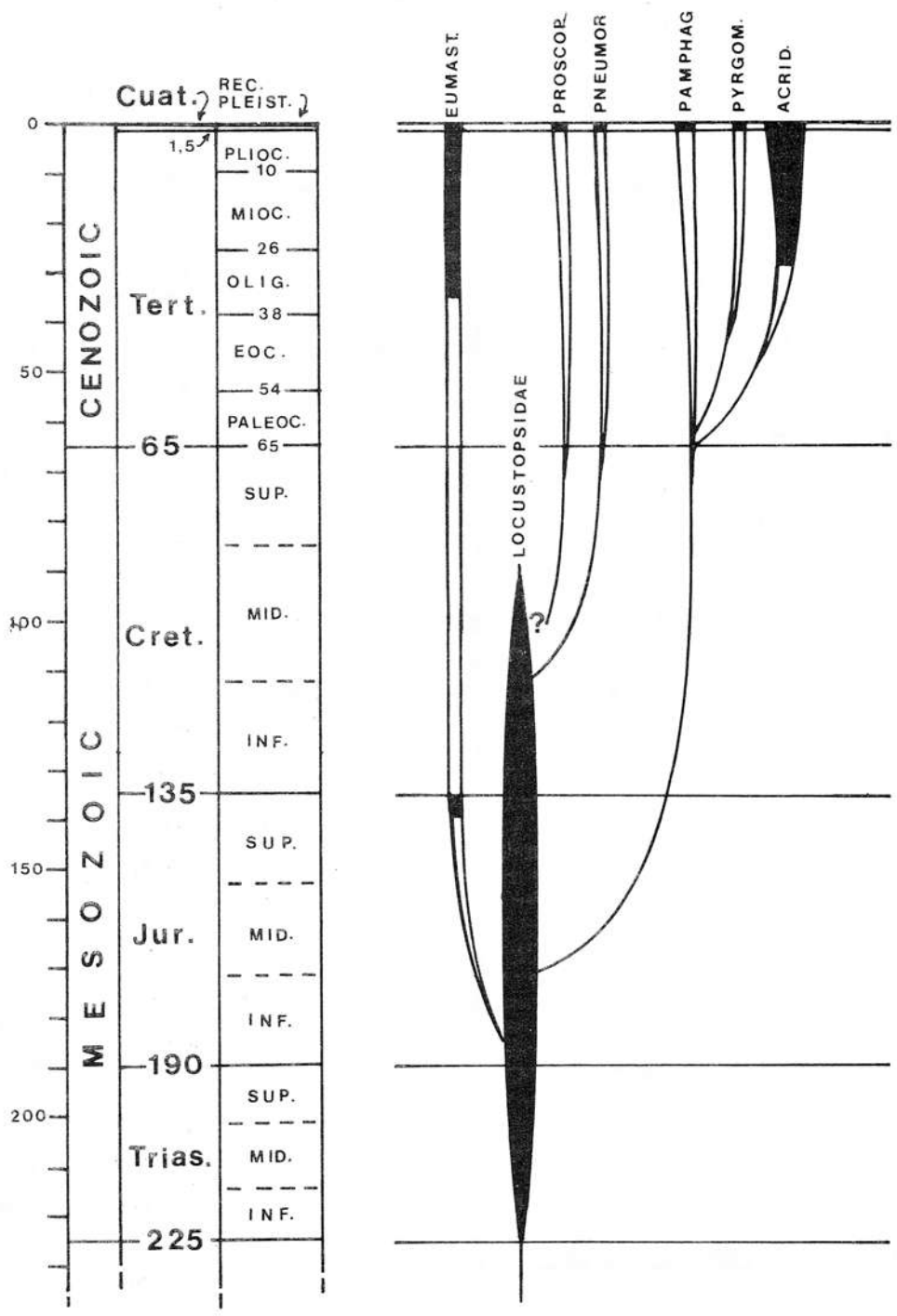


Fig. 8. Phylogeny of the Acridomorpha (After Sharov, 1968). The Locustopsidae are shown as the basic stock of all recent acridomorph groups. Numbers represent millions of years to the present.

Tristiridae. This family was first defined by Rehn (1942) and later in a more comprehensive way by Amedegnato (1974). It is evidently of South American origin. In the mentioned paper by Amedegnato, it is evident that, by a typographical error, two pyrgomorphid genera, *Algete* and *Deraspiella* are repeated at the beginning of the list of tristirids genera, while *Bufonacris, Chilacris,* and *Crites* have been omitted. Our own studies agree with Amedegnato's opinion in assigning to this group the rank of family.

The geographical origin and dispersion center of the Tristiridae is located in the southern part of South America (Patagonia and south Chile), where there exists at present the greatest concentration of genera and species. Having their origin in a temperate to cold climate, these insects have been able to migrate north only through the highlands of the Andes, reaching Peru (and maybe Ecuador) through the restricted regions of favorable climate. Rehn (loc. cit.) thinks that the tristirids are an ancient group, and says that the beginning of their evolution must antedate the start of the Andean orogenesis (that is, pre-Pliocene).

The tristirids as a group are probably much older than that. Even if the evidence of phyletic relationships of this group with other acridomorphs is still obscure, it seems plausible that, as in the case of the proscopiids, the tristirids may come from a primitive acridomorph stock located in South America since early mesozoic times.

Pauliniidae. Little can be said about this family, to which only two genera *(Paulinia)* and *Marellia)* have been assigned. Study of the genitalia of these two genera creates doubts about their close relationship. *Paulinia* seems, so far, to be monotypic, and a number of species have been assigned to *Marellia,* though these species are difficult to separate. The external similarity of these two genera may be due to convergence by adaptation to the aquatic habitat. Both have much the same distribution in tropical and subtropical South America. The pauliniids might be related to the Acrididae.

Romaleidae. Of the group of autochtronous South American families, the romaleids, with 63 genera, represent the largest and most diversified family. The great adaptive radiation of the romaleids is shown by their invasion of diverse habitats ranging from xerophilous, semi-arid conditions *(Alcamenes),* to the dendrophilous forms of the tropical rain forest *(Trybliophorus, Nautia, Ophthalmolampis).* I consider this family as it has been defined by Amedegnato (1974), with the exception of the tribe Aucacrini, that I include with the Ommexechidae. The Aucacrini seem to be a sort of bridge between the two families. Roberts (1941), when erecting the subfamily Romaleinae, indicated that it was probably of ancient origin.

Judging by its distribution and affinity with the Ommexechidae, the Romaleidae seem to have their geographical origin in the southern temperate and subtropical zone. From an evolutionary viewpoint, they have been more successful than the Ommexechidae, and a number of the genera have adapted very well to the tropical jungle, and have spread through the Amazon basin and the Guiana Shield. Probably after the establishment of the Panamanian bridge or maybe before, through island chains, they invaded Central America, Mexico, and the southern part of the Nearctic region *(Brachystola, Dracotettix, Litoscirtus, Phrynotettix, Romalea, Taeniopoda, Tytthotyle).* Such generic diversification in the Neartic region suggests an early invasion of the North American continent.

Ommexechidae. The composition of this family has been the subject of controversy, especially regarding some groups which differ in structure from *Ommexecha* and closely related genera. I agree with the composition proposed by Eades (1961), including in this family all the genera now listed by Amedegnato (1964) plus the tribe Aucacrini which she puts in Romaleidae (excepting *Quitus,* which I believe not to be a valid genus, being based in a unidentifiable nymph). Mesa (1963) gives reasons derived from caryology and phallic characters for assigning family rank to the ommexechids.

Roberts (1941), Eades (1961), and Amedegnato (1974) state that the Ommexechidae and the Romaleidae are closely related, and the first of these authors also indicates that the Ommexechidae are the most divergent branch of the Cryptosacci. Ronderos (1972, 1973a,b,c, 1974) in the course of an excellent revision of this family, also adopts the composition and classification of this family proposed by Eades (1961).

The Ommexechidae are autochthonous South American acridoids. Their origin and distribution center is located in the southern temperate to subtropical zone (middle and northern Argentina, Uruguay, Paraguay, southern Brazil). A few species reach north, invading the tropics. Members of *Ommexecha* and the monotypic genus *Descampsacris* are found in the Amazon basin and north of it, at least in Colombia.

FAMILIES BELONGING TO THE WORLD FAUNA OF ACRIDOMORPHA

The three families that follow (Eumastacidae, Pyrgomorphidae, and Acrididae) are world-wide in distribution. This sets them apart from the preceding ones, that not only are exclusively Neotropical (with the exception of Romaleidae, that has invaded the south of the Nearctic region), but also seem to be autochthonous to South America. The members of these three families can be separated into two clear-cut groups according to their apparent origin. The first of these groups includes the Eumastacidae, the Pyrgomorphidae, and five subfamilies of Acrididae: Melanoplinae, Cyrtacanthacridinae, Acridinae, Gomphocerinae, and Oedipodinae. All these families and subfamilies, while forming a systematically heterogeneous group, share the common character of being outsiders of either Neartic or Old World affinities, which invaded the Neotropical region probably during the Cenozoic and South America in late Cenozoic times.

The second, taxonomically more homogeneous, of these groups includes the remaining five subfamilies of Acrididae (Proctolabinae, Copiocerinae, Leyptysminae, Rhytidochrotinae, and Ommatolampinae). This group differs from the preceding one in that all of its members are typically Neotropical. Some have stray representatives in the southern part of this region, neither have they been found anywhere in the Old World. All of them are prevalently tropical and, according to their particular distribution, their centers of evolution must have been either in Central America or northern South America (Guiana Shield), whence most of them have spread into the Amazon basin. A brief discussion of each of these families and subfamilies follows.

Eumastacidae (sensu lato). The great antiquity of the Eumastacidae has already been mentioned. They diverge considerably from the rest of the acridomorphs, as has been shown by Sharov and other authors.

Ragge (1955) thinks that, in the Upper Paleozoic, some 225 million years ago, the eumastacids were already differentiated as a line that diverged from the rest of the Caelifera. According to Sharov (1968), these insects arose from the Locustopsidae during the Lower Jurassic, and he describes a new genus *(Archaeomastax)* from the Upper Jurassic of Kara Tau (U.S.S.R., east of the Aral Sea) that would be the oldest known acridomorph belonging to a recent group. Apart from this genus, fossil Eumastacidae are not known until the Pliocene. In North America, fossil eumastacids have been found in the Oligocene of British Columbia and in the Miocene of Florissant, Colorado (Rehn, 1948).

The great antiquity of the eumastacids seems to be beyond doubt. Blackith (1973) gives additional proof of this antiquity, such as the frequent association of eumastacids and Pteridophyta (ferns), on which many species live and feed, and he lists several primitive anatomical characters. According to this author, a Paleo-Mesozoic origin of the eumastacids is necessary to explain their present distribution on the basis of a pangeic origin, possibly in the Africa+Madagascar+India general area. Also according to this author, multivariant analysis of the characters of recent groups and also cytological studies support the notion of great antiquity of this group. Descamps (1973a,b) agrees, and he makes additional contributions in support of it. He points out the great diversity of the structures of the abdominal terminalia and the genitalia, which make necessary a division of the family into several different groups, which suggests a long evolution.

Once the antiquity and corresponding diversity of the eumastacids is established, the question remains of when and how they reached the Neotropical region. Descamps (1973b) reaches the conclusion that the American Eumastacidae *(sensu lato)* are related

to those of the Oriental region, and must have invaded America from Eastern Asia in the Mesozoic (through the Bering Bridge, according to his map). Two different groups from the said region invaded America: first the ancestors of the Cryptophalli, and later those of the Stenophalli. These early eumastacids settled in the Caribbean region, which became a secondary evolution center for them. The invasion of South America must have occurred (Descamps, loc. cit.) during the Cretaceous (probably near its end, through island chains?) on two successive occasions: first came the Morseinae and Temnomastacinae, which are the subfamilies which now reach farthest south, and then the rest of the subfamilies, that remain to this day circumscribed to northern South America and the Amazon basin (besides Central America).

The already mentioned findings of a fossil Oligocene eumastacid in British Columbia, and of a Miocene one in Florissant, Colorado, support the idea of an invasion from Asia, via Bering.

Pyrgomorphidae. Among the Acridoidea *(s.str.)*, the family Pyrgomorphidae seems to be one of the oldest. According to Sharov (1968), the Pyrgomorphidae and Acrididae arose from pamphagid stock at the beginning of the Cenozoic ((fig. 8). Dirsh (1975) attributes great antiquity to pyrgomorphids, suggesting that these insects originated at an early age from pre-acridid stock. Rehn (1951) also indicates that pyrgomorphids belong to an ancient line of acridoids.

Concerning the geographical origin of the pyrgomorphids, Rehn (1951, 1953) points to Gondwana as the most probable place, and remarks that the area Africa+Madagascar is the richest in species, and that the Oriental region stands second to it. Kevan (1964, 1965) points to the pan-tropical distribution of these insects and indicates that the Ethiopian region plus Madagascar is the richest in genera and species and hence could be their main evolution center, but also remarks that the greatest number of tribes are represented in the south Asiatic region, and that the origin of the family could, for this reason, be Oriental as well. If the origin of the pyrgomorphids were Upper Triassic, before the breakup of Pangaea, a duality of evolutionary centers would be unnecessary for explaining their present distribution since the origin of the pyrgomorphids could be located within the territory that enclosed the then united oriental Africa, Madagascar, and India.

In the Americas the Pyrgomorphids are located mainly in Mexico, Central America, and northern South America, with ten genera in Mexico + Central America, and five in South America (Kevan 1964). Also according to Kevan (1964, 1965), the American pyrgomorphids show affinities with those of southeastern Asia, and must have reached America from there (through the Bering bridge) in two or three separate invasions.

In this way, American pyrgomorphids would be, like the American eumastacids, invaders from S.E. Asia. Their very limited success in South America (only five genera) points to a rather recent (Pleistocene) invasion of this continent.

Acrididae. The family Acrididae presents a peculiar case. Of the ten subfamilies represented within the Neotropical region, there are four (Melanoplinae, Acridinae, Gomphocerinae, and Oedipodinae) wich are clearly late invaders from the Nearctic region, with connections with the rest of the Holarctic region and Old World fauna in general. Another of its subfamilies, the Cyrtacanthacridinae, is prevalently an Old World group, with ethiopic and pan tropical relationships. The five remaining subfamilies (Proctolabinae, Copiocerinae, Leptysminae, Rhytidochrotinae, and Ommatolampinae) are exclusively neotropical, but their centers of evolution and distribution are located in Central America and the northern part of South America. From there, some of them spread to the south of the Nearctic region and the West Indies, most of them to the Amazon basin, and a few even to the south temperate zone of South America. The fact that all these subfamilies belong to the family Acrididae which is of world-wide distribution, together with their north-neotropical location, seems to indicate for them a relatively ancient origin and migration from an unknown part of the world. Their present habitat also suggests that, whatever the place they came from, it must have had a tropical climate, since they are prevalently tropical. A few remarks on each of the acridid subfamilies follow.

Proctolabinae. According to the recent paper by Descamps (1976) this subfamily, with 22 known genera, has a Central American and Amazonian distribution. Ten of its

genera are of Central American distribution (reaching southern Mexico); another ten are Amazonian and the remaining two inhabit both regions. Only one of the Amazonian genera reaches south as far as Mato Grosso and Paraguay. According to this author, most of the Central American genera are rather primitive, while the Amazonian ones are on the whole, more evolved.

Copiocerinae. Most of this subfamily (tribe Copiocerini) is northern South American and Amazonian, with two genera *(Adimantus, Chlorohipus)* reaching the southern subtropical zone. The other tribe, Aleuini, has a peculiar distribution, with most of its species (genera *Aleuas* and *Zygoclistron*) in the southern subtropical to temperate zone, and a single known species of *Zygoclistron* north of the Amazon River at Mount Roraima.

Leptysminae. This subfamily has an ample distribution within the Neotropical region, and has spread northward to the south of the Nearctic region *(Leptysma).* Its tribe Leptysmini is the most widely distributed, extending from Uruguay and corresponding latitudes of Argentina to southern United States. The Chloropseustini is typically Amazonian and the Tetrataeniini goes all the way from southern Mexico and Central America to the south of the Amazonian basin, with at least one genus *(Haroldgrantia)* reaching the southern temperate zone in Uruguay and Argentina.

Rhytidochrotinae. Most of its 15 genera are from northern South America *(Colombia),* with one of them reaching north to Central America *(Piezops),* one to Ecuador *(Paropaon),* one to Peru *(Rhytidochrota),* and one even to Central Brazil *(Lathacris).* Its center of evolution is northern South America.

Ommatolampinae. With 46 known genera, this subfamily is considerably larger than any of the preceding ones. It reaches north to the southern U.S.A. *(Clematodes)* and south to Uruguay and corresponding latitudes of Argentina *(Abracris).* It has also invaded the West Indies *(Dellia, Caletes).* Most of its genera, however, are located in northern South America and the Amazon basin, and some of them are Central American.

Cyrtacanthacridinae. This subfamily presents peculiarities that set it apart from the rest of the Neotropical acridids. As a whole, it has some 30 genera distributed throughout the tropics and subtropics of the world. In the Americas it is represented only by *Halmenus,* in the Galapagos Islands, and *Schistocerca,* with a number of species throughout the tropical and subtropical parts of the Americas. *Schistocerca* also has a single species in Africa.

This distribution is difficult to explain within our present knowledge. Judging only by the genus *Schistocerca* it would seem that it is of South American origin, and that a single species reached Africa and became established there. The fact that the large majority of the cyrtacanthacridines belong to the Old World fauna seems to invalidate this explanation. As a provisional hypothesis at least, it could be proposed that the genus *Schistocerca* was originally African, and that the common ancestor of the African and American species reached the Americas in some undetermined age. This hypothetical *Schistocerca* found in America favorable conditions that lead to considerable speciation, while its African counterpart was severely limited in its possibilities by the other cyrtacanthacridine genera and species that already occupied all the favorable niches. Even if among the species of *Schistocerca* are some of the best fliers of all the acridids, how and when this hypothetical ancestor of the American species reached the New World is a matter for further speculation.

Melanoplinae. According to Rehn & Randell (1963), the melanoplines are of Neartic origin, and its primary center of distribution is Laurentian. From there they spread to the palearctic (via the Bering bridge) and the Neotropical regions, reaching South America through the Panamanian land bridge. The Neotropical melanoplines are certainly invaders from the north, and, among them, the South American ones would be post-Pliocene migrants.

By reason of their origin in a region of temperate climate, these insects invaded South America through the highlands of the Andes, thus avoiding tropical conditions, and only were able to leave these high-lands when they reached the subtropical and temperate zone in the south of the continent. There they underwent a considerable adaptive radiation (Rehn, 1954; Carbonell & Ronderos, 1973; Rowell & Carbonell, 1977). According to Rehn (1954), the two secondary centers of evolution of the melanoplines

on the South American continent are in the Colombian-Venezuelan Andes and in that region of South America south of the 15th. parallel to south central Argentina and Chile.

The melanoplines, with more than 20 known Neotropical genera, are at present an important faunal element in this region, especially throughout the Andes and in the southern part of South America. With one known exception, they have been unable to colonize the humid tropical jungle. They stop in the marginal and transitional regions. The Neotropical melanoplines are currently being revised by Ronderos and by Ronderos & Carbonell.

Acridinae. Also recent invaders from the Neartic region, the Neotropical acridines have spread with moderate success to South America, where they probably arrived during the post-Miocene. The Neotropical elements of this subfamily have not been the subject of any recent revisionary study that would throw light on their affinities and possible relationships with other acridines of the world. Coming from the Nearctic region, they must be related in some way to the Old World acridine fauna. It is interesting to note that one of its species, *Metaleptea brevicornis* (L.) is the only known acridomorph that reaches all the way from Canada to Argentina and Uruguay.

Gomphocerinae. As in the preceding case, the Neotropical gomphocerines seem to be Neartic invaders. The South American ones probably came through Panama after the union of the continents. Some 30 genera are known from the Neotropical region. In a recent study of the Gomphocerinae of the world, Jago (1971) analyzes the relationships of the different genera. According to his study, the Neotropical gomphocerines seem to be related to the Asian species through the Nearctic fauna. This suggests a rather recent (Cenozoic) distribution of Eastern Asia - Bering - North America - Central America - South America pattern. A few cases of apparent neotropical ethiopic relationship are mentioned, which could be relicts of a larger distribution via Europe or Asia, rather than an indication of direct relationship with the Neotropical and Ethiopian faunas, which seems unlikely for modern acridids of this group. An interesting case is that of *Dichromorpha.* This genus has the species *D. viridis* in North America and the similar *D. australis* in southern South America, separated by an enormous expanse of territory where 17 has never been found.

Oedipodinae. The oedipodines are inhabitants of the drier, temperate to tropical regions throughout the world. They are poorly represented in the Neotropical region (seven genera). All of these Neotropical representatives have clearly Nearctic affinities. The invasion of South America by the oedipodines must be very recent, maybe during the Pleistocene. The most common oedipodine species in South America belongs to the North American genus *Trimerotropis,* and, though several specific names are applied to it in different regions, it is probably a single species ranging from Colombia to southern Argentina and Chile, and is abundant from the Andean Altiplano to sea level under arid conditions. The other six genera are located in the northern part of South America, in Central America, and the West Indies.

FAUNAL STRATA IN THE ACRIDOMORPHS OF THE NEOTROPICAL REGION

The Neotropical acridomorph fauna, according to the above, seems to be grouped roughly into three different faunal strata.

The oldest of these strata is formed by the families Proscopiidae, Tristiridae, Ommexechidae, and Romaleidae. The family Pauliniidae should perhaps be added to the preceding unless it proves to be related to the Acrididae. These families seem to be autochthonous South American insects, that is, descendants of acridomorph or pre-acridomorph sotck already existing in the South American part of Gondwana prior to its breaking away from the rest of the Gondwanian lands. Their evolution and distribution centers are located in different parts of southern South America. Three different lineages seem to be represented among them (exclusive of the Pauliniidae). The oldest and most divergent from the rest of the acridomorphs are the Proscopiidae. They

are followed by the Tristiridae, which are less ancient and closer to the rest of the acridoids. The Ommexechidae and Romaleidae together represent the third lineage, more evolved and probably less ancient than the tristirids.

A second and probably more recent stratum is formed by a series of subfamilies of Acrididae which are exclusively Neotropical (though some have representatives in the south of the Nearctic region). They are the Proctolabinae, Copiocerinae, Leptysminae, Rhytidochrotinae, and Ommatolampinae. Their evolution and distribution centers are located in Central America and northern South America (Guiana Shield), and they have envaded, as a rule, the Amazon basin. All are composed of tropical species, only a few of these species having become established in subtropical or temperate regions. Considering that the family Acrididae, to which they belong, is widespread throughout the world, it may be postulated that these Neotropical subfamilies are the descendants of tropical acridids that came to, or were originally located in, the southern, tropical part of the North American continent. From there, these acridids invaded Central America when conditions after its emergence permitted, and later they migrated to South America, probably as waif emigrants, through island chains, in several invasions beginning in early Cenozoic times.

An alternate explanation that seems less plausible is that these acridids belong to a relatively ancient stock common to tropical Africa and northern South America. The Guiana Shield did not become separated from Africa until Lower Cretaceous times, being the last part of South America to lose contact with the African continent. In order to accept this theory, a considerable antiquity for the Acrididae as a family must be postulated, which seems unlikely. In this case, the nearest relatives of these Neotropical subfamilies of Acrididae in the recent fauna should be found in tropical Africa and, to my knowledge, they have not been located so far. The time elapsed from Lower Cretaceous times to the present (120-130 million years) seems long enough for considerable evolution to have taken place and, hence, relationships in recent forms would be difficult to locate.

To this group of acridid subfamilies belong most of the dendrophilous forms of the tropical jungle (Central America, Guianas, Amazon basin). The richess of this dendrophilous fauna suggests that these insects have undergone the same mechanism of speciation by isolation in "refuges" during the Pleistocene glaciations which has been described for other sectors of the Amazonian fauna (Haffer, 1967; Turner, 1975; Vanzolini & Williams, 1970; Vuilleumier, 1971).

A last and very heterogeneous stratum must be added to the preceding ones. The only common feature of the elements in this third stratum is that all of them seem to have invaded the Neotropical region in relatively recent times, and the South American part of it probably in late Cenozoic, about the time of the completion of the Panamanian land bridge in Mid-Pliocene or later. To this stratum belong the Eumastacidae, Pyrgomorphidae, and several of the subfamilies of the Acrididae, namely, the Melanoplinae, Acridinae, Gomphocerinae, and Oedipodinae. To these perhaps the Cyrtacanthacridinae should be added, but the time of their invasion of the Neotropical region seems difficult to estimate. Obviously, three different lineages are included in this stratum. A very old one is represented by the Eumastacidae; a relatively more modern but still ancient one by the Pyrgomorphidae; and a third one in which all the modern and more evolved lines of Neotropical Acrididae are put together.

Within this last stratum of relatively recent invaders, the eumastacids are tropical, the pyrgomorphids tropical and subtropical, while the included subfamilies of Acrididae are, in general, originally of temperate climates. Among these Acrididae of the neotropical fauna, different degrees of adaptation to tropical conditions can be discerned.

SUMMARY

Any attempt at interpretation of the origin, evolution, and distribution of the Neotropical acridomorph fauna was, until recently, practically impossible because of the very imperfect knowledge of their systematics. A number of recent works on the subject have clarified it to the point of making at least a preliminary hypothesis feasible.

Progress in the geophysical sciences during the last fifteen years, especially in the displacements of the continents after the close of the Paleozoic, has an important bearing on the history of the Neotropical region. Also, recent advances in the paleogeography, stratigraphy, and paleontology of this region substantially help our undestanding of the biota.

The recently acquired information on the effects of the Pleistocene glaciations on the South American continent and their influence on the climatic and vegetation zones and on the evolution and speciation of many Neotropical animal and plant groups cannot be ignored anymore in studies of the evolution and distribution of the Neotropical fauna.

Putting together all the mentioned elements, plus what is known of the past history, phylogeny, and systematic relationships of the acridomorphs themselves, a preliminary hypothesis is made on the origin, evolution, and distribution of the Neotropical fauna of these insects.

The Neotropical acridomorph fauna, according to this hypothesis, can be roughly divided into three strata, taking into account mainly their probable origin and history, their present distribution, and the assumed length of their presence in the Neotropical region.

The first of these strata is formed by the Proscopiidae, Tristiridae, Ommexechidae, and Romaleidae. They are postulated as the descendants of acridomorph or pre-acridomorph stock that was already in the South American part of Gondwana before it broke away from the rest of the lands of that supercontinent. Out of this common origin has arisen this evidently heterogeneous stratum. The proscopiids are probably much older and more primitive than the rest and also systematically removed from them. Of the three remaining families, the Tristiridae are the older group, the Ommexechidae-Romaleidae assemblage being far more evolved. To this same stratum, the family Pauliniidae, of uncertain affinities, should perhaps be added.

The second stratum, much more homogeneous than the other two, is formed by the five subfamilies of Acrididae that are exclusively Neotropical (Proctolabinae, Copiocerinae, Leytusminae, Rhytidochrotinae, and Ommatolampinae). Those subfamilies, as revealed by their present distribution, seem to have their evolution and distribution centers in Central America and the northern part of South America, whence they spread mainly to the Amazon basin and elsewhere in some cases. They are of tropical lineage, and may represent an early branch of the Acrididae that established in the southern or tropical part of the North American continent and that invaded, also at an early epoch, the northern part of South America. Or they may have descended from African-Guyanan acridid stock which remained in the Guiana Shield after its separation from Africa. But the last of these tentative explanations seems the less probable because it implies a considerable antiquity for this stock and relationships with the African fauna that have not yet been demostrated.

The third and most recent of the faunal strata is taxonomically and in terms of the origin of its elements heterogeneous. These elements, however, have in common evident relationships with the faunas of the rest of the world. For this reason they are put together as the most recent elements of the acridomorph fauna of the neotropical region, which they must have reached in relatively modern times. As for the South American part of this region, must of them seem to have invaded it during the Late Cenozoic (Pliocene and post-Pliocene) times. In this stratum are included the very ancient group of the eumastacids, the more recent one of the pyrgomorphids, and the remaining subfamilies of the Acrididae (Melanoplinae, Cyrtacanthacridinae, Acridinae, Gomphocerinae, and Oedipodinae), which are more evolved than the proceding families.

RESUMEN

Una interpretación del origen, la evolución y la zoogeografía de la fauna neotropical de acridomorfos, resultaba prácticamente imposible hasta hace muy poco tiempo, a causa de un conocimiento muy imperfecto de su sistemática. Un cierto número de trabajos recientes sobre este tema lo han clarificado considerablemente, hasta el punto de hacer posible por lo menos una hipótesis preliminar.

El progreso de los conocimientos geofísicos en los últimos quince años, especialmente en lo que se relaciona con la deriva continental después del paleozoico, es asimismo de gran utilidad para comprender la distribución de las faunas pasadas o actuales, y tiene gran significación para la historia de la región neotropical. Asimismo, el progreso reciente de la paleogeografía, estratigrafía y paleontología de esta región, contribuyen en forma substancial a nuestro conocimiento de su biota.

La información obtenida en los últimos años, sobre los efectos de las glaciaciones del pleistoceno en el continente sudamericano, y su influencia sobre las zonas climáticas y formaciones vegetales y, en consecuencia, sobre la evolución y especiación de muchos grupos de animales y plantas neotropicales, no puede ser ignorada de ahora en adelante en futuros estudios sobre la evolución de la fauna neotropical.

Reuniendo todos los elementos mencionados y la información disponible sobre la historia, filogenia y afinidades de los acridomorfos, se ha formulado una hipótesis preliminar sobre el origen, evolución y distribución geográfica de la fauna neotropical de estos insectos.

La fauna neotropical de acridomorfos, de acuerdo a esta hipótesis, puede ser dividida, a grandes rasgos, en tres estratos faunísticos, de acuerdo principalmente a su origen probable, su historia, su distribución geográfica actual, y el tiempo estimado de su presencia en la región neotropical.

El primero y más antiguo de estos estratos estaría formado por las familias Proscopiidae, Tristiridae, Ommexechidae y Romaleidae. Se postula para estas familias su descendencia de antepasados acridomorfos o pre-acridomorfos que ya estaban presentes en la parte sudamericana de Gondwana, antes de que se separara del resto de las tierras de dicho supercontinente. Fuera de esta supuesta comunidad de origen territorial, este estrato es evidentemente heterogéneo. Los proscópidos son verosimilmente más antiguos y primitivos que el resto, y están asimismo alejados de los demás desde el punto de vista taxonómico. De las familias restantes, Tristiridae es la más antigua; el conjunto Ommexechidae-Romaleidae es más evolucionado. A este estrato quizá deba agregarse Pauliinidae, de afinidades inciertas.

El segundo estrato, mucho más homogeneo que los otros dos, está formado por las cinco subfamilias de Acrididae (Proctolabinae, Copiocerinae, Leptysminae, Rhytidochrotinae y Ommatolampinae) que son exclusivamente neotropicales. Estas subfamilias, tal como lo revela su distribución actual, deben haber tenido sus centros evolutivos y de distribución en América Central y la parte norte de la América del Sur (Escudo Guayanense), desde donde se dispersaron principalmente a la cuenca amazónica, y en algunos casos también a otras regiones. Todos estos acridios son de clima tropical, y podrían representar una línea primitiva de Acrididae, establecida tempranamente en la parte meridional de la América del Norte, y restringida al principio a esta zona por razones climáticas. Estos insectos invadieron muy pronto la parte septentrional de la América del Sur. Otra posible alternativa es la de que estos insectos desciendan de una línea de acridios afro-guayanense, que quedó en la parte septentrional de América del Sur cuando su separación del Africa. Pero esta última explicación parece la menos probable, ya que implica una considerable antiguedad de esta línea de Acrididae, y relaciones con la fauna africana que no han sido encontradas aún.

El tercero y mas reciente de los estratos faunísticos es, desde el punto de vista taxonómico, y también en lo relacionado con el origen de sus elementos, el más heterogéneo. Estos elementos que lo forman sin embargo, tienen en común las características de su evidente relación con las faunas del resto del mundo, y de representar además la parte mas reciente de la fauna de acridomorfos de la región neotropical, a la cual deben haber llegado, en su mayor parte, en época relativamente moderna. En lo que concierne a la parte sudamericana de dicha región, la mayoría de los elementos de este estrato deben haber llegado a ella a fines del cenozoico (plioceno y posteriormente). En este estrato se reúnen el grupo arcaico de los Eumastacidae, los Pyrgomorphidae que son seguramente mas recientes, y las subfamilias de Acrididae que no han sido incluidas en el estrato anterior (Melanoplinae, Cyrtacanthacridinae, Acridinae, Gomphocerinae y Oedipodinae) mucho más evolucionadas en su onjunto que las mencionadas anteriormente.

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